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Granivory: patterns, processes, and consequences of seed consumption on two continents

Granivoría: patrones, procesos y consecuencias del consumo de semillas en dos continentes

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ABSTRACT

Because seeds are free-living juvenile plants that are killed and eaten by seed-eating animals, granivory is in many respects more similar to predation among animals than to most other kinds of herbivory. Community-level consequences of granivore-plant interactions have been best documented in desert ecosystems in North America, where experimental manipulations have been instrumental in documenting the ecological roles of different species and functional groups, the mutual regulation of granivore and plant populations by direct predator-prey interaction, and the indirect effects of this interaction on the structure and dynamics of communities. The presence of the same functional groups and sometimes the same genera of seed-eaters and plants suggests that many aspects of ecological interactions are similar in North and South America. Differences in the biotas have been hypothesized to have had important evolutionary and coevolutionary consequences. The absence of diverse, specialized seed-eating desert rodents in South America has been attributed to the presence of now-extinct small, bipedal marsupials that may have been ecologically similar to North American kangaroo rats. It has also been suggested that South American desert plants may exhibit traits reflecting their evolution in the absence of specialized mammalian granivores. Intercontinental comparisons and additional descriptive and experimental work in South American deserts should greatly increase understanding of ecological processes and permit more rigorous evaluation of evolutionary and coevolutionary hypotheses.

Key words: Ant, bird, coevolution, competition, granivory, indirect interaction, predation, rodent, seed.

RESUMEN

Dado que las semillas son plantas juveniles de vida libre que son muertas y consumidas por animales comedores de ellas, la granivoría es, en muchos respectos, más similar a la depredación entre animales que a los otros tipos de herbivoría. Las consecuencias a nivel comunitario de la interacción granívoro-planta han sido bien documentadas en ecosistemas de desierto en Norteamérica. Aquí, las manipulaciones experimentales han sido fundamentales para la documentación de los papeles ecológicos de diferentes especies y de grupos funcionales, y de la regulación mutua entre poblaciones de granívoros y plantas por interacciones directas depredador-presa y por efectos indirectos de esta interacción sobre la estructura y dinámica de las comunidades. La presencia de los mismos grupos funcionales, y a veces de los mismos géneros de plantas y comedores de semillas, sugiere que muchos aspectos de la interacción granívoro-planta son similares en Norte y Sudamérica. Se ha propuesto que diferencias existentes entre las respectivas biota tendrían importantes consecuencias evolutivas y coevolutivas. La ausencia en Sudamérica de roedores desertícolas granívoros, especializados y diversos, se ha atribuido a la existencia de los ahora extintos marsupiales bípedos que podrían haber sido ecológicamente similares a las ratas canguro norteamericanas. También se ha sugerido que las plantas sudamericanas de desierto podrían exhibir tendencias que reflejen su evolución en ausencia de mamíferos granívoros especializados. Comparaciones intercontinentales y trabajo experimental y descriptivo adicional en los desiertos sudamericanos debieran incrementar grandemente la comprensión de procesos ecológicos y permitir una evaluación más rigurosa de las hipótesis evolutivas y coevolutivas propuestas.

Palabras claves: Hormiga, ave, coevolución, competencia, granivoría, interacción indirecta, depredación, roedor, semilla.

INTRODUCTION

Seeds are the complete, free-living juvenile stages of higher plants. Like many other juvenile stages that contain an embryo and stored nutrient reserves to sustain subsequent growth and development, seeds represent a concentrated source of energy and other essential nutrients. It is not surprising, therefore, that several different kinds of animals have specialized to varying degrees to find, collect, and consume seeds,

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or that the depredations of these granivorous animals have major effects on the ecology and evolution of seed plants.

Several features of assemblages of plants and their seed predators have made these excellent systems to investigate the ecological dynamics and evolutionary consequences of interactions between trophic levels. Perhaps most importantly, the system lends itself to precise quantification and experimental manipulation under a variety of conditions, from highly controlled laboratory environments to natural field situations.

Like most other interactions between organisms in different trophic levels, granivory has been studied at a variety of levels in the ecological hierarchy: from the foraging behavior of individual animals, to the ecological dynamics and evolutionary adaptations of single-species populations, to the interaction and coevolution of plant and animal populations, to the process of seed consumption and its consequences for the organization of communities and the function of ecosystems. Unfortunately, many of these studies were conducted by different investigators on different systems to answer different questions. Most of them provide valuable insights into the process of granivory, but often the information is too fragmentary and diffuse for useful synthesis.

The present paper is restricted almost entirely to granivory in desert ecosystems, in part because most of our own experience and much of the research on these topics on both continents has been in arid habitats, and in part because such a narrow focus permits a more detailed and integrated understanding of the ecological processes and evolutionary consequences of granivory as a complex, community-level interaction among several species on different trophic levels. We review what is known about the nature of seed resources, the kinds of animals that feed on them, patterns of interspecific interaction and community organization and the impacts of granivores on ecosystem function in both North and South America. Although the physical environments, seed-eating animals, and seed-producing plants of North and South American deserts are similar in many respects, the long history of geographic isolation of South America has resulted in the evolution of a unique biota. These distinctive plants and animals provide opportunities to assess the evolutionary and coevolutionary consequences of ecological interactions between trophic levels.

THE COMPONENTS

Seed resources

The seed resources that are the specialized prey of granivores are only one stage in the life cycle of desert plants. On the one hand, the seed plays several crucial roles in the life history. In addition to being the first free-living juvenile stage, the dormant seed is typically the only stage capable of dispersal and the stage best able to tolerate temporarily unfavorable environmental conditions. One apparent reason why granivory is so conspicuous in desert ecosystems is that the seed stage is particularly important in the life cycle of desert plants. A large fraction of the desert flora is characterized by annual or ephemeral life histories. These plants survive the long, unfavorable dry periods between rains as dormant seeds buried in the soil. They germinate and complete the vegetative and reproductive parts of their life cycles during the brief, unpredictable periods when the soil is wet. Since a large proportion of the flora spends the vast majority of its life as seeds, there are always many seeds potentially available to granivores (*e.g.*, Tevis 1985c, French *et al.* 1974, Nelson & Chew 1977, Reichman 1984). Certain traits of the seeds of many desert plant species may reflect adaptations to prevent or reduce consumption by certain classes of granivores.

On the other hand, because the seed is only one stage in the plant life cycle and because attributes of the seed affect the growth rate, probability of survival, and reproductive allocation of later stages, it would be misleading to suggest that all seed traits reflect adaptations to avoid predation. On the contrary, the attributes of the seeds of each plant species probably represent a complex compromise among diverse and often conflicting selective pressures acting on all phases of the life cycle. For example, seed size strongly affects susceptibility to predation by most classes of granivores, but is equally important in influencing seedling size and hence growth rate, competitive ability, and probability of survival of the young plant. Selection for seed size undoubtedly reflects a compromise among these different and often conflicting costs and benefits.

Different solutions to these diverse and sometimes opposing selective forces acting on different phases of the life cycle probably account in large part for the enormous variety of seeds. Seeds vary greatly in size, shape, chemical composition, physical structure, and time and place of their production and dissemination (*e.g.*, Baker 1972). Although in arid environments seeds do not realize the extremes of either dust-sized orchid seeds or coconuts, the variety is impressive. In North American deserts seed size varies by at least 5 orders of magnitude, from those of ephemeral annuals that weigh on the order of 10^{-5} g to those of perennial shrubs that weigh more than 1 g. These seeds can be spherical, flat, or elongate; smooth or adorned with various kinds of surface irregularities or projections. They differ in hardness, thickness of seed coat, and the relative content of oil, carbohydrate, protein, and secondary compounds. Virtually all desert seed crops are sporadic, but they differ greatly in their amplitude, timing and productivity. A few desert plants have fleshy fruits or other obvious adaptations for dispersal by animals. For most plant species the negative effect of granivores as predators probably outweighs any mutualistic effect of granivores in seed dissemination, but the patterns and mechanisms of seed dispersal in desert ecosystems warrant further study.

From the limited work that has been done, the diversity of seeds in arid regions of South America is not demonstrably different from North America. In fact, many of the important genera of both annual (*e.g.*, *Sphaeralcea, Lepidium, Descurainia, Nama, Phacelia, Erodium, Pectis, Portulaca, Crypthantha, Nicotiana, Verbesinia, Euphorbia,* and *Solanum*) and perennial (*e.g.*, *Larrea, Cercidium, Lycium, Ambrosia, Encelia, Flourensia, Celtis, Gutierrezia, Acacia,* and *Prosopis*) are shared between desert regions on the two continents. Although quantitative data are lacking, within these genera seeds appear to be of similar size and shape in North and South America. This conservatism suggests that constraints related to evolutionary history have inhibited divergence in response to local selective pressures.

Despite these apparent similarities, the possibility that there may be significant quantitative differences in the morphology and chemistry of seeds, both between closely related species and between the floras as a whole, on the two continents should be investigated. There is considerable circumstantial evidence that predation by granivores plays a major coevolutionary role in maintaining the diversity of seed types within the North American desert flora. Because the profitability of different kinds of seeds to consumers depends on the efficiency with which they can be found, collected, processed, and assimilated, seed morphology and chemistry play a large part in determining susceptibility of seeds to various classes of granivores (*e.g.*, Pulliam & Brand 1975, Rissing 1981, 1986). Mares & Rosenzweig (1978) have suggested that in the absence of specialized granivorous rodents South American plants may have been able to evolve seeds that are more resistant to predation by other classes of granivores. Their hypothesis would predict that the desert annual flora of South America would exhibit a different range of seed shapes and sizes than their North American counterparts.

Granivores

A large variety of organisms obtain some or all of their nutrition from seeds. Many of these, such as certain mammals, birds, and ants are unspecialized omnivores that feed opportunistically on seeds. Others, such as bruchid beetles, lygaeid bugs, and other insects, are often highly specialized to locate and attack seeds before they have ripened and dispersed from the parent plant. Still others, such as fungi, consume seeds while they are buried in the soil or in the caches of granivores. All of these kinds of seed consumers are potentially important in ecological and evolutionary interactions between plants and higher trophic levels, but they will not be considered further in this paper.

This leaves those seed consumers that are traditionally considered to be granivores: those animals that are specialized to find, collect, process, and consume individual dry seeds after they have dispersed from the parent plant. In North American deserts, as in most arid habitats throughout the world, there are three major classes of these granivores: rodents, birds, and insects.

Attributes of these seed-eaters are summarized in Table 1 and reviewed in detail elsewhere (Brown *et al.* 1979a). Only some relevant traits will be considered further here. Granivorous rodents, ants, and birds are all well represented in arid North America, although the sparrows and quail are not such obligate and specialized seed-eaters as the finches, parrots, sand grouse, and doves in other desert regions (a few species of doves are also important granivores in North America).

The ecological interactions of each class appear to be distinctly different and to depend on unique features of their foraging behavior. Rodents and birds are similar in being large-sized, endothermic, relatively aseasonal granivores that are particularly efficient at exploiting large and clumped seeds. They differ in that rodents are nocturnal, relatively sedentary, central-place, caching foragers that locate buried seeds by olfactory and tactile cues, whereas birds are diurnal, highly mobile foragers that locate surface seeds visually and do not store food. Ants are similar to rodents in some respects, but differ in being primarily diurnal, highly seasonal, single-load foragers that can often economically harvest very small and highly dispersed, but not deeply buried seeds. Birds and ants are similar in being diurnal, single-load, predominately surface-feeding foragers, but they differ in most other respects. Because of these similarities and differences in foraging behavior, each class of granivores overlaps substantially in some aspects of resource use but differs significantly in others.

The same three classes of specialized animals are present in South America, but the number of species in each group that are largely or exclusively granivorous show some important differences between the continents. Granivorous rodents are much less well represented in South America (Mares 1975, 1985, Mares *et al.* 1977, Glanz 1982). All of the native North American desert rodent genera are absent from South America; the endemic South American rodents are less diverse in genera and species, and none of these forms appear to be such specialized granivores as are the North American genera *Dipodomys, Perognathus,* and *Microdipodops* (Table 1; Mares 1976, 1985, Meserve & Glanz 1978, Pizzimenti & De Salle 1980, Meserve 1981a, b, Glanz 1982). The pattern in ants is different. The same dominant genera are present on both continents (Table 1), but species richness appears to be substantially lower in South America than in comparable habitats in North America (Hunt, cited in Mares *et al.* 1977, Bucher 1980). Birds show yet another pattern (Bucher 1980, Capurro & Bucher 1982, Olrog 1984). Although some of the granivorous bird genera are different in South America, diversity of avian seed-eaters appears to be at least as great as in North America (Table 1). With a few important exceptions, the South American representatives of the three classes of granivores appear to be subject to the same behavioral constraints and play similar ecological roles to their North American counterparts (Table 1).

TABLE 1

Comparison of the major groups of granivorous animals in arid zones of North and South America

Comparación de los principales grupos de animales granívoros en zonas áridas de Norte y Sudamérica

	Rodents	Ants	Birds
NORTH AMERICA			
Dominant genera of specialized granivores	*Dipodomys* *Perognathus* *Chaetodipus* *Microdipodops*	*Pogonomyrmex* *Pheidole* *Veromessor*	*Callipepla* *Zenaida* *Columbina* *Spizella* *Amphispiza* *Aimophila* *Pipilo*
Other genera	*Peromyscus* *Reithrodontomys*	*Novomessor* *Solenopsis*	*Pooecetes* *Chondestes* *Cardinalis* *Eremophila*

Table 1 (Cont.)

	Rodents	Ants	Birds
Individual body size	7-120 g	0.5-15 mg	10-200 g
Social organization	Solitary	Large colonies	Solitary to large flocks
Foraging strategy	Individual; multiple load	Individual or column; single load	Individual or flock; single load
Seed storage	Frequent	Frequent	None
Mobility of individuals	$\sim 10^2$ m	$\sim 10^1$ m	$\sim 10^1-10^3$ km
Thermoregulation	Endothermic	Ectothermic	Endothermic
Daily activity	Nocturnal	Temperature-dependent, but mostly diurnal	Diurnal
Seasonal activity	Year-round or hibernate	Highly seasonal	Year-round, but migratory
Maximum longevity	2-5 years	Workers: months, colonies: > 10 years	2-10 years
SOUTH AMERICA			
Dominant genera of specialized granivores	None	*Pogonomyrmex* *Pheidole*	*Eudromia* *Nothura* *Zenaida* *Columba* *Columbina* *Cyanoliseus* *Myopsitta* *Junco* *Diuca*
Other genera	*Phyllotis* *Oryzomys* *Eligmodontia?*	*Solenopsis*	*Saltator* *Poospiza* *Sicalis* *Paroaria* *Sporophila* *Saltatricula* *Phrygilus*
Individual body size	19-70 g	0.5 mg	10-250 g
Social organization	Solitary	Large colonies	Flocks or solitary; mixed species flocks in winter
Foraging strategy	Individual; multiple load	Individual or column; single load	Individual or flock; single load
Seed storage	Some?	Probably	None?
Mobility of individuals	$\sim 10^2$ m	$\sim 10^1$ m	$\sim 10^1-10^3$ km
Thermoregulation	Endothermic	Ectothermic	Endothermic
Daily activity	Nocturnal or crepuscular	Temperature-dependent but mostly diurnal	Diurnal
Seasonal activity	Mostly year-round	Seasonal	Year-round, but migratory
Maximum longevity	10-18 months	Workers: short-lived; colonies: many years	Unknown

The differences and similarities between North and South America in the diversity, degree of specialization, and other attributes of granivores offer great opportunities for comparative studies in evolutionary ecology. Most of the remainder of this paper will be devoted to exploring some of the consequences of these differences for the ecological interactions among species, the structure and dynamics of arid ecosystems, and the coevolution of relationships between interacting species.

ECOLOGICAL INTERACTIONS

Granivory as Predation

Granivores are predators. They seek out, capture, eat, and kill their prey, the dormant juvenile individuals of seed plants. In this respect they differ from most other "herbivores" that often do not kill their food plants because they consume only certain vegetative or reproductive structures. As a consequence, the relationship between granivores and plants is in many respects more similar to predator-prey interactions between animal species than to other kinds of plant-animal interactions. In particular, granivores recognize individual seeds as discrete prey items, and by collecting, moving, and killing juvenile individuals they have direct effects on the abundance and distribution of their prey. In contrast, many folivorous animals have quite different effects on food plant populations, because they do not recognize individual plants as discrete units of resource and their feeding activities directly affect the biomass and fitness, but not the number and distribution of individual plants. For example, many phytophagous insects spend their entire lives feeding on a small part of a single plant, whereas grazing mammals may feed on several individuals of small plants simultaneously.

Effects of Granivory in North American Deserts

Many of the implications of granivory as a predator-prey interaction remain to be explored, even in North America where most of the research has been conducted. For example, concepts such as predator switching and functional and numerical responses might be applied to develop realistic models to predict the dynamics of granivore and plant populations in the field. Although this degree of sophistication has not yet been attained, a recent workshop on granivory (held at the University of California at Los Angeles in 1985) emphasized just how much has been learned in the last two decades, mostly as a result of research in the North American desert.

The traditional view, which stems from the work of Went (1948, 1949, Went & Westergaard 1949), Tevis (1958a, b, c), and others, suggested that the struggle to survive the physical stresses of the harsh desert climate so dominates the ecology of desert plants that biotic interactions of all kinds have little effect on the abundance and distribution of individuals or the composition of plant communities. Furthermore, seeds were supposed to be so abundant in desert soils as to make it improbable that any granivores are ever food-limited, again presumably because the animals are limited by the stressful physical environment rather than by interactions with other organisms. Thus, this view would hold that seed predation by animals is of virtually no importance in the ecology of desert ecosystems at any level from the regulation of plant and animal populations to the determination of species composition and pathways of energy and nutrient transfer.

It is becoming increasingly clear just how incorrect this perception was. Populations of both seed plants and seed-eating animals are indeed limited both ultimately and proximally by physical factors. Of these the most important is almost certainly the availability of water, which directly limits germination, growth, and reproduction of the plants and indirectly limits survival and reproduction of the animals through effects on their food supply (*e.g.*, Beatley 1969, Reichman & Van DeGraff 1975, Dunning & Brown 1982, Kenagy & Bartholomew 1985). However, the physical effects of water, sunlight, temperature, nutrients, and other factors are not independent of biotic interactions within and between species. On the contrary, plants compete intra- and interspecifically for the limited water (*e.g.*, Inouye 1980, Inouye *et al.* 1980, Fonteyn & Mahall 1981, Robberecht *et al.* 1983), availability of seeds limits populations of granivores (*e.g.*, Brown 1973, 1975, Pulliam 1975, Davidson

1977a, b, Pulliam & Parker 1979, Dunning & Brown 1982, Brown & Munger 1985), animals compete intra- and interspecifically for the limited seeds (Brown & Davidson 1977, Davidson 1977a, b, 1980, 1985, Brown *et al.* 1979b, 1986, Munger & Brown 1981, Ryti & Case 1984, 1986, Brown & Munger 1985), and predation by granivorous animals limits the abundance, distribution, and species composition of the seed plants (Brown & Davidson 1977, 1986, Brown *et al.* 1979b, 1986, Inouye *et al.* 1980, Davidson *et al.* 1984, 1985). Furthermore, indirect interactions involving three or more species of plants and granivores can also be shown to be important in determining the structure and dynamics of desert communities (*e.g.* Inouye *et al.* 1980, Inouye 1981, Davidson 1980, 1985, Davidson *et al.* 1985, Brown *et al.* 1986).

It is only possible to summarize some of the most dramatic consequences of the biotic interactions here. The best evidence comes from controlled, replicated experiments in which selected species or functional groups of granivores or plants have been removed or exogenous seeds have been added. Experiments have been conducted in both the Sonoran and Chihuahuan Deserts of southern Arizona (see Brown *et al.* 1986 and included references for details). The most spectacular result is that some large-seeded annual plant species have increased literally thousands of times, changing from fugitive to dominant species on plots from which granivorous rodents have been removed (summarized in Brown *et al.* 1986). This response has been observed at three different sites, and at some of these it has been accompanied by major indirect effects as well (see below). These results show some of the effects of direct predator-prey interactions on the prey populations. Interestingly, manipulation of prey availability by adding supplemental millet seed had much less dramatic effects on the granivore populations, although a significant increase in one rodent population (*Dipodomys spectabilis*) and in foraging by granivorous sparrows suggested that at least some species were food-limited (Brown & Munger 1985, Thompson & Brown in preparation).

From the standpoint of ecological theory and the effect of interactions between trophic levels on the structure and dynamics of communities and ecosystems, perhaps the most exciting result of the experiments is the large number of indirect effects that have been caused by a small number of perturbations. Below we describe briefly those indirect interactions that have been best documented. These provide examples of most of the simple pathways linking three or four species that have been analyzed in the theoretical literature and are illustrated in Pianka's paper in this symposium.

1. Addition of seeds caused an increase in the largest rodent species, *Dipodomys spectabilis,* which then supressed populations of the two next largest species, *D. merriami* and *D. ordii,* by aggressive interference (Brown Munger 1985, Bowers *et al.* 1987).

2. Removal of *D. spectabilis* showed that interference from this species changed microhabitat use by two other *Dipodomys* species, which in turn affected microhabitat use by still smaller rodents (Bowers *et al.* 1987).

3. Responses of ants to removal of the large harvester ant, *Pogonomyrmex rugosus,* provided additional evidence (see Davidson 1980) that this species aggressively excluded intermediate-sized *Pogonomyirmex desertorum* from the vicinity of its mounds. This created refuges for the even smaller *Pheidole xerophila,* which competed exploitatively with *Pogonomyrmex desertoryum* (Davidson 1985). These results confirmed the relative magnitudes of the net interactions predicted by Davidson (1980).

4. When released from predation by removal of rodents, large-seeded plants increased in density, eventually dominating winter annual communities and suppressing densities of small-seeded plants (Davidson *et al.* 1984, 1985).

5. In the Sonoran Desert, decreases in the densities of small-seeded plants in indirect response to removal of rodents (above) resulted in a decline in ant colonies (Davidson *et al.* 1984). In the Chihuahuan Desert, removal of rodents led indirectly to a decrease in *Erodium abertianum,* which caused a decline of the ant *Pogonomyrmex desertorum,* that feeds primarily on its seeds (Davidson *et al.* 1985).

6. The large-seeded annual *Erodium cicutarium* increased in response to removal of rodents, and this resulted in greatly increased incidence of infection by the specific pathogenic fungus *Synchytrium papillatum* (Inouye 1981). This is an example

of exploitative competition, which is an indirect interaction. This case is particularly interesting because the two competitors exploit entirely different stages of the life cycle of their common prey; the fungus consumes vegetative plants whereas the rodents feed on seeds. Other examples of interspecific competition, but among granivores, are cited above.

7. Long-term removal of rodents resulted in significantly decreased foraging by birds (Thompson & Brown in prep.). Two hypotheses to account for these effects are being evaluated: changes in plant species composition caused by rodent predation, and changes in microhabitat structure caused by rodent foraging and digging.

8. Rodent populations, especially the dominant kangaroo rats, are sustained primarily by feeding on middle-sized seeds, but they forage preferentially for large seeds (Brown & Davidson 1977, Reichman 1977, 1978). The result is that plant species with middle-sized seeds supress large-seeded species by maintaining dense populations of their rodent predators. In comparison to the Sonoran Desert site, in the Chihuahuan Desert where productivity and rodent populations were higher, the rodents kept large-seeded annual plants at substantially lower densities, and these preferred prey showed much greater increases when rodents were removed (Brown *et al.* 1986). This is an example of Holt's (1977) "apparent competition", and one way that plants with smaller seeds counteract the strong asymmetrical competition of large-seeded species.

These experimental results appear to have at least three important implications for predator-prey interactions and community organization. First, regulation of local abundance and distribution of both consumers and producers cannot be understood adequately in terms of single abiotic factors or biotic interactions. Because a network of complex interactions links species and functional groups, community structure and dynamics reflect the combined effects of many interactions, both strong and weak, and both direct and indirect. Moreover, fluctuations in the physical environment, rather than diminishing the impact of biotic relationships, interact with them to affect their outcomes. Second, interactions along different pathways are resolved in distinctive temporal sequences. Since indirect pathways with two or more links have inherent time delays, they are usually resolved more slowly than direct competitive or predator-prey interactions. Thus, among both ants and rodents, effects of direct interference preceded those of exploitative competition mediated through plant (seed) populations. Similarly, exploitative competition between ants and rodents was expressed before more indirect facilitation. This temporal pattern has important implications for the use of manipulative experiments to understand community processes. Short-term experiments will tend consistently to overestimate the importance of interference competition and predation, relative to exploitative competition and even more indirect interactions. The fact that the densities of many species are still changing in response to manipulations begun at our Chihuahuan Desert site in 1977 suggests that long-term experiments will be required to elucidate the structure and dynamics of any reasonably complex ecological system.

Finally, many of the most important properties of ecosystems, including maintenance of species diversity and resilience in response to perturbations, must depend on the network of interactions. For example, our results show that some short-term impacts of our manipulations are eventually reversed by processes operating through indirect pathways; for example, short-term competitive interactions among rodents, ants, and birds are later offset by indirect facilitation. If it is generally true that the net effects of indirect interactions tend to be opposite in sign and approximately equal in magnitude to the direct interactions (*e.g.*, Davidson *et al.* 1984, Brown *et al.* 1986, Sterner 1986), then the indirect pathways confer an important kind of dynamic stability upon the community as a whole. The resistance and resilience of ecosystems to both natural fluctuations and artificial perturbations may depend importantly on the properties of the networks of interactions.

These experimental results demonstrate that in North American deserts granivory is an extremely important interaction. At a mininum it plays a major role in determining the abundance, biomass, and species composition of at least annual plants, seed-eating animals, and certain other kinds of organisms (*e.g.*, a parasitic fungus). It is likely that the interaction also has important direct effects on perennial plants and indirect effects on many other organisms (*e.g.*, phytophagous insects), but these have not yet been detected either because they would appear only after long time lags or because the response of the organisms to the experimental manipulations has not been studied. Clearly the granivore-plant interaction affects not only the functional organization of the food subweb incorporating those species directly involved; by affecting at a minimun the pattern of dominance in the entire annual plant community, it also importantly influences the abundances and distributions of many other species and the pathways through which energy and materials flow through desert ecosystems.

Comparisons Between South and North America

Much less is known about the interaction between granivores and plants in South American deserts. It is possible to make at least some very general predictions based on our North American experience. These predictions can sometimes be evaluated tentatively in the light of the limited, primarily descriptive data that are available. More importantly, we hope that these speculations will stimulate experimental work in South America that eventually will make possible much more insightful comparisons between the two continents. On the one hand, some features of granivory should be similar between the two continents because: 1) they are necessary consequences of the dynamics of predator-prey interactions; 2) they reflect similar constraints on attributes of seeds as a consequence of the limitations on plant reproductive strategies; 3) they reflect similar constraints on granivores owing to foraging economics and other processes (Table 1); and/or 4) they reflect similar (in some cases convergent; see Mares 1976) adaptations of both plants and animals to similar environments. On the other hand, within the limits set by these common constraints, we would expect important differences between the two continents because of the important differences in the identity, diversity, and degree of specialization of the granivores— and probably of the plants as well.

Since the differences in the components have a long evolutionary history, it is difficult to distinguish purely ecological effects from those that are owing at least in part to evolutionary and coevolutionary responses. Nevertheless, it should be possible to perform similar kinds of manipulative experiments in South America, to document the responses of plants, granivores, and other selected kinds of organisms, and then to interpret these results, both in terms of strictly ecological dynamics with reference only to the South American system being studied (as is done above and in the references cited for North America), and in terms of evolutionary and coevolutionary processes by comparisons between South and North American systems.

COEVOLUTIONARY RELATIONSHIPS

Sorting, Evolution, or Coevolution?

At least in North American deserts, it is clear that granivore-plant interactions are so strong that population dynamics and community structure of both predators and prey are substantially affected by simple experimental manipulations of both seed-eaters and their food plants. Since the effects of the interacting species on the survival and reproduction of each other are so great, there are potentially important opportunities for coevolution. Since granivory is a predator-prey interaction, coevolution would be expected to be a continual race, with the granivores evolving adaptations that enhance their abilities to find and process seeds and the plants evolving mechanisms to prevent their seeds from being harvested and eaten. But to what extent and at what level does such coevolution actually occur?

It is difficult to do experiments on coevolution, and in the absence of controlled manipulation it is difficult to tell whether the mechanisms that allow predator and prey to coexist are the result of: 1) ecological sorting out from a large pool of species that could potentially occur together, the subset of species that have traits that enable them to coexist locally with each other; 2) independent evolution of attributes in one species that increase its fitness in the presence of the other without a reciprocal response in the interacting species (evolution, but not coevolution); or 3) continued and reciprocal incorporation of characteristics by each species in response to the changes in the other species (coevolution).

This is not a trivial problem. Although there may be cases where close interactions are largely restricted to particular pairs of species that obviously affect each other's fitness and show apparent reciprocal adaptations, most granivore-plant and other interspecific interactions are much more complex. The interactions take place in the context of a diverse community with many species of both predators and prey. This makes it difficult to identify unambiguously the specific effects of individual species on each other and to assign apparent adaptations to these selective forces. In fact it seems important to question whether coevolution, if it occurs at all, is a process that occurs primarily between particular pairs of species, or whether it is a more general process that occurs at a more diffuse level with each individual species evolving in response to the collective selective pressures exerted by all of the species with which it interacts sufficiently to affect its fitness.

Our own opinion is that although many of the attributes of both granivores and plants reflect primarily ecological accomodation and unilateral evolution, many of them also reflect coevolution– not as a simple pairwise process, but instead as a complex process of mutual change involving spatially and temporally varying assemblages of many interacting species.

Evidence for Coevolution in North America

Coevolution between plants and the animals that consume and disperse their seeds has been studied intensively in both mesic habitats in eastern North America and tropical habitats of Central America. Despite all of the work on granivory in deserts, however, there has been relatively little work on coevolutionary aspects of the interaction. Perhaps this is because there are few examples of close, obviously coevolved relationships between particular kinds of seeds and granivores. For example, seed dispersal mutualisms are conspicuous in many habitats, including arid regions elsewhere in the world, but not in the North American deserts. There are important exceptions, however. Many cacti and some perennial shrubs (*e.g.*, *Prosopis, Celtis,* and *Lycium*) have sweet, brightly colored, fleshy fruits that are eaten by birds that disperse the seeds. At least one large annual, *Datura,* has seeds that are clearly adapted for ant dispersal. O'Dowd & Hay (1980) showed that the relatively large seeds of this species are extremely hard, but they have a fleshy, energy-rich food body attached. Ants collect the seeds and transport them to their nests where they remove the food body and discard the seed in sites that tend to be favorable for germination. O'Dowd & Hay (1980) also showed that by removing the concentrations of newly dropped seeds from around the parent plant, the ants substantially reduced seed predation by rodents. Since this mode of seed dispersal is common in other habitats, including the arid zone of Australia, it is puzzling why it should be so rare in arid regions of North America.

The other evidence for coevolution of gravivores and their food plants in arid North America involves the sizes, shapes, and perhaps chemical composition of seeds in relation to the food-finding and processing constraints on different kinds of granivores. Best developed by Pulliam & Brand (1975) for arid grasslands, the general idea is that because the profitability of seeds to different kinds of granivores depends largely on seed morphology, plants in particular environments tend to evolve seed traits that make them less profitable for the granivores that are most likely to be present in those environments. For the grasslands of southeastern Arizona, where ants are active in the summer and migrant finches are abundant in the winter, Pulliam & Brand (1975) noted that smooth, hard forb seeds that were difficult for ants to transport were produced in the spring and early summer, whereas long grass seeds with awns or other structures that increased handling time for birds were produced primarily in the fall. It should be possible to generalize these arguments to other habitats and other kinds of plants and granivores, such as rodents, which may be prevalent in them.

However, there are several problems in rigorously testing this idea. First, it is important to distinguish between adaptations and constraints. In southern Arizona grasslands most forbs have C_3 photosynthetic pathways, grow during the cool winter and spring seasons, and belong to genera and families that tend to have smooth, round, hard seeds, whereas grasses typically have C_4 photosynthesis, grow during the hot summer months, and have elongated seeds with complex structures. Thus we might expect the same seasonal distribution of seed morphologies that Pulliam & Brand (1975) observed, even in the absence of all granivores. Second it is important to distinguish between ecological sorting and coevolution. Have plant species with particular seed morphologies in relation to their phenologies simply been able to colonize grassland habitats because traits that they already possessed (*i.e*, preadaptations) gave them sufficient protection from predation, or did they evolve the seed traits after invading the grasslands in response to local patterns of granivory? Third, there is the question of whether these traits represent unilateral evolutionary responses of the plants to the granivores, or reciprocal adaptations by both partners in the interaction. Finally there is the difficulty in attributing particular seed traits unambiguously to a single selective force, when there is good reason to believe that seed morpholopy influences many aspects of plant fitness and may well represent a compromise between many different and sometimes opposing selective pressures.

Despite these difficulties, it would be unwise to dismiss the role of coevolution in determining, at least in part, many attributes of both seeds and granivores. There is abundant evidence that seed traits, especially size and shape, strongly influence the profitability of seeds to different classes of granivores and that selective foraging with respect to these traits profoundly affects the survival of seeds. These are necessary preconditions for coevolution. Given that they are met in almost every habitat, it would be surprising if there were not some significant coevolution, no matter how difficult it may be to document. One of the best evidences of coevolution would be correlated spatial variation in traits of both seeds and granivores, either within particular species or by replacement of species to form predictably different communities. Little work of this kind has been done within North American deserts.

Granivore-plant Coevolution in South America: the Mares and Rosenzweig Hypothesis

Intercontinental comparisons offer some of the best opportunities to study coevolution. Largely because of historical events (*e.g.*, see Mares 1985), physically similar environments on different continents often have strikingly different biotas; because of longstanding barriers to dispersal, entire taxonomic or functional groups that are dominant in one region may be reduced or even totally absent in another. The involvement of different kinds of organisms with different constraints in predator-prey and other interactions means that coevolution on different continents might be subject to very different selective pressures and consequently proceed in quite different directions. If enough is known about the identity and characteristics of the components, it may be possible to frame and test *a priori* predictions about the outcome of such coevolution.

Mares & Rosenzweig (1978) have made such predictions about the coevolution of granivores and plants in North and South America. These are based on the very low diversity of granivorous rodents in the deserts of South America and differences in the rates of removal of seeds in duplicate experiments conducted in similar habitats on both continents (see also Mares 1975, 1976, Meserve 1981a). From this information and what is known from North America about food preferences in relation to seed attributes, Mares & Rosenzweig (1978) predicted certain characteristics of the flora and seeds in South American deserts. The detailed basis of these predictions is complicated by several factors, including the past occurrence in South America of a group of extinct marsupials of the family Argyrolagidae (Simpson 1970) that are superficially similar to kangaroo rats and might represent the now-missing specialized granivorous small mammals. Several points need to be clarified in order to make precise *a priori* predictions from the Mares & Rosenzweig (1978) hypothesis. Nevertheless, there is no doubt that the composition of granivores is substantially different in the arid regions of North and South America, and it seems important to test the speculation that there may be corresponding differences in the plants, especially the annuals, that would reflect the independent coevolution of granivore-plant interactions on the two continents.

Detailed studies of granivory in South American deserts that emphasize the attributes and roles of the plants appear to offer great promise, especially when the results are synthesized with what is already known about the granivorous animals and compared with the very different systems that have been so well studied in North America.

CONCLUSIONS

At a workshop on granivory held at the University of California at Los Angeles in 1985, the participants declined to publish the proceedings. The consensus was that enormous progress has been made in the last two decades. The old view that biotic interactions in general, and granivory in particular, are unimportant in deserts has been corrected. Our knowledge of the nature of granivore-plant interactions, the ecologically important attributes of the component organisms, and the impact of granivory on arid ecosystems has increased greatly. Nevertheless, much of the information is too diffuse and fragmentary to permit a synthetic overview of this producer-consumer interaction, even within the North American deserts where most of the work has been done. Because even less is known about granivory in South America, definitive intercontinental comparisons and comprehensive syntheses are even more difficult. We have not attempted such a treatment.

Nevertheless, we believe that the opportunities for research, especially in South America, are enormous. Systems of seeds and their predators provide excellent material for both ecological experiments and comparative evolutionary studies. Application of these approaches to South American organisms and habitats should provide invaluable information that will not only be of great interest in its own right, but also will acquire added importance when it is interpreted in the light of comparable information for similar systems in North America and elsewhere.

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